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NANNOCHARAX MACULICAUDA, A NEW SPECIES OF AFRICAN CHARACOID FISH (CHARACOIDEA: DISTICHODONTIDAE) WITH COMMENTS ON THE GENUS *HEMIGRAMMOCHARAX*

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Abstract.—A new species of African characoid of the genus *Nannocharax* is described from the upper Ivindo River system of Gabon. The high longitudinal scale count, elongate body form, and absence of marked head and body pigmentation other than a prominent caudal peduncle spot distinguish this species within the monophyletic assemblage formed by *Nannocharax* and *Hemigrammocharax* within the Distichodontidae. The validity of the currently used diagnostic character for *Hemigrammocharax* is discussed.

Introduction

As discussed by Vari (1979:332) the phylogenetic relationships within the monophyletic assemblage formed by *Nannocharax* and *Hemigrammocharax* of the Distichodontidae remain unresolved. The current distinction between these genera is based solely on the extent of the pored lateral line, a character of questionable validity both diagnostically and phylogenetically. Nonetheless, given the absence of a satisfactory subdivision of the group formed by these genera, the new species described here is assigned to *Nannocharax* in keeping with its possession of the traditional diagnostic character for the genus—a completely pored lateral line.

Nannocharax maculicauda, new species

Holotype.—MNHN (Muséum National d'Histoire Naturelle) 1981-608, 30.2 mm standard length (SL), collected September 2, 1964, by J. and G. Géry, in a still side arm of the upper Ivindo River opposite Bourassié, Gabon, at the juncture of the Djouah and Karouaga Rivers (approx. 1°20′N, 13°12′E) (see station 17, Géry, 1965:376–377).

Paratypes.—7 specimens (USNM [National Museum of Natural History] 224524, 3 specimens [1 cleared and stained], 23.5–28.7 mm SL; MNHN 1981-609, 1 specimen, 24.0 mm SL; Géry collection, 2 specimens, 23.1–23.3 mm SL; BM(NH) [British Museum (Natural History)] 1981-3.30:1, 1 specimen, 23.0 mm SL) taken with the holotype.

Diagnosis.—Within *Nannocharax*, the relatively high lateral-line count

Fig. 1. *Nannocharax maculicauda*, holotype, MNHN 1981-608, 30.2 mm SL.

(55–61 pored lateral-line scales between the lateral-line origin and the hypural joint) readily distinguishes *N. maculicauda* from all its congeners with the exception of *N. intermedius* (lateral line 47–55), *N. lineomaculatus* (45–53), *N. luapulae* (50), *N. niloticus* (50–55), and *N. occidentalis* (50–56). *Nannocharax maculicauda* can be distinguished from all of the above species by the large, longitudinally elongate ovoid dark spot on its caudal peduncle, a pigmentation pattern not found in the other species in the genus. The new species also lacks the vertical cross-bars found on the body in *N. intermedius, N. luapulae* and *N. niloticus* and the lateral midside stripes or spots or a combination of such pigmentation patterns that characterize *N. lineomaculatus* and *N. occidentialis*.

Among those species assigned to *Hemigrammocharax* by various authors (see Poll 1967, table opposite p. 124) only *H. ocellicauda* has a reported longitudinal scale count approximating that of *Nannocharax maculicauda*. Boulenger (1907:485) reported 50 longitudinal scales for *H. ocellicauda*. However, examination of the two syntypes of *H. ocellicauda,* which are in poor condition, reveals only about 43 longitudinal scale pockets plus 3 scales on the caudal fin (G. J. Howes, pers. comm.). Although sharing a similar pigmentation pattern, *Nannocharax maculicauda* differs from *Hemigrammocharax ocellicauda* in its possession of a completely pored lateral line, in its transverse scale row count (6½–7 scales above lateral line and 4½–5 below, in contrast to 6½ and 8½ for *H. ocellicauda*), and in body depth (5.9–6.7 in SL, in contrast to 4.9–5.3 for *H. ocellicauda*).

Description.—Table 1 gives a summary of morphometrics of the holotype and paratypes. Body elongate, sides slightly compressed, greatest body depth at anterior dorsal-fin origin. Predorsal body profile very slightly convex to interorbital region, straight to snout. Body profile at base of rayed dorsal fin straight, slightly posteroventrally sloped. Dorsal body profile posterior to rayed dorsal fin straight to caudal peduncle. Ventral body profile gently convex from tip of lower jaw to below pectoral-fin insertion, nearly

Table 1.—Morphometrics of *Nannocharax maculicauda*, new species. Standard length is expressed in mm. Measurements 1 to 10 are percentages of standard length; 11 to 14 are percentages of head length.

		Holotype	Paratype (6) Range	Paratype (6) Average
	Standard length	30.2	23.3–28.7	24.5
1	Greatest body depth	17.0	15.0–17.0	16.2
2	Snout to dorsal-fin origin	51.0	49.0–51.0	50.0
3	Snout to anal-fin origin	77.0	75.0–77.0	75.8
4	Snout to pelvic-fin origin	49.0	47.0–49.0	48.3
5	Snout to anus	70.0	67.0–69.0	67.8
6	Origin of rayed dorsal to hypural joint	51.0	51.0–53.0	52.0
7	Least depth of caudal peduncle	8.0	7.0–8.0	7.3
8	Pectoral-fin length	14.0	14.0–15.0	14.3
9	Pelvic-fin length	16.0	15.0–17.0	15.8
10	Head length	27.0	28.0–29.0	28.8
11	Orbital diameter	36.0	34.0–37.0	35.2
12	Snout length	27.0	24.0–27.0	25.3
13	Postorbital length	39.0	39.0–40.0	39.8
14	Interorbital width	22.0	20.0–22.0	21.2

straight from there to anus. Anal-fin base straight, slightly posterodorsally inclined. Head elongate, snout acute, conic; tip of snout overhangs anterior edge of lower jaw. Mouth relatively small. Nares large, approximate; anterior opening circular, posterior larger, crescent shaped. Eye diameter large relative to head length. Pupil ovoid, with pronounced anterior emargination of iris (Figs. 1 and 2).

Jaw teeth bicuspidate, in a single functional series in each jaw. 7 or 8 teeth on each dentary, tooth size gradually decreasing posteriorly; dentary replacement teeth arranged in a single series within an enlarged dentary replacement-tooth trench. Dentary movably attached to lateral surface of anterodorsal portion of angulo-articular (Fig. 3), without a laterosensory canal segment. Dentaries immovably joined syndesmotically along medial surfaces. Premaxilla with 6 or 7 teeth, tooth size gradually decreasing posteriorly, ultimate premaxillary tooth approximately one-third length of longest; a single series of partially formed replacement teeth embedded in flesh of inner surface of premaxilla. Premaxillae immovably attached syndesmotically along their medial surfaces; joined premaxillae mobile with respect to ethmoid region. Maxilla edentulous, posterior portion flat, plate-like (Fig. 4), extending nearly completely beneath first infraorbital bone when mouth is closed. Ectopterygoid toothless. Third, fourth and fifth infrapharyngobranchials and fifth ceratobranchial (lower pharyngeal) bearing patches of posteriorly-recurved, simple teeth. Gill rakers 3+6 on first gill-arch in

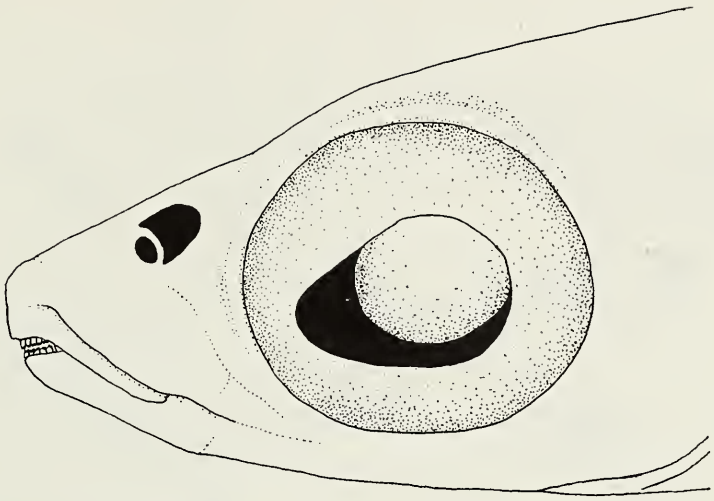

Fig. 2. Left lateral view of the head of *Nannocharax maculicauda*.

cleared and stained specimen. Branchiostegal rays 4; 3 rays attached to ceratohyal, 1 to epihyal. Gill membranes adherent to isthmus anteriorly. Frontoparietal fontanel extending slightly anterior of epiphyseal bar. Antorbital triangular, well ossified. First infraorbital large, plate-like with a branched laterosensory canal segment, covering most of maxilla laterally when mouth is closed. Second infraorbital having the form of a triangular plate anteriorly, only tube of laterosensory canal ossified posteriorly. Infraorbitals 3, 4 and 5 poorly developed, only laterosensory canal tubes ossified in largest specimens. Ossified portion of opercle reduced dorsally. Postcleithrum 1 lacking, postcleithra 2 and 3 fused into a single, ventrally curved element (Vari 1979, Fig. 35).

Scales ctenoid with 9 to 11 ctenii formed by a series of independent ossifications along edge of main body of scale; lateral line interrupted ("stutters") in 3 smallest specimens, complete in larger specimens. Scales in a longitudinal series 61 in holotype (59 in 5 paratypes, 58 in 1 paratype, 55 in 1 paratype); 0 to 2 pored lateral-line scales posterior to hypural joint; scale rows above lateral line to origin of rayed dorsal fin 7 in holotype (7 in 4 paratypes, 6½ in 3 paratypes); scale rows below lateral line to anal-fin origin 5 in holotype (5 in 3 paratypes, 4½ in 4 paratypes). Body scales extending in a triangular pattern onto middle rays of caudal fin.

Dorsal fin pointed, anterior rays longest; dorsal-fin rays iii-9-i in holotype (first unbranched ray very small) (ii-9-i in 3 paratypes, iii-9-i in 1 paratype, ii-8-i in 3 paratypes); dorsal-fin origin approximately on vertical through pelvic fin insertion. Anal fin emarginate, anal-fin rays ii-10-i in holotype (ii-10-1 in 1 paratype, ii-10 in 1 paratype, ii-9-i in 5 paratypes). Pectoral fin pointed, first ray longest, reaching two-thirds distance to pelvic-fin origin; pectoral-fin rays 12 in all specimens. Longest pelvic-fin rays reaching three-

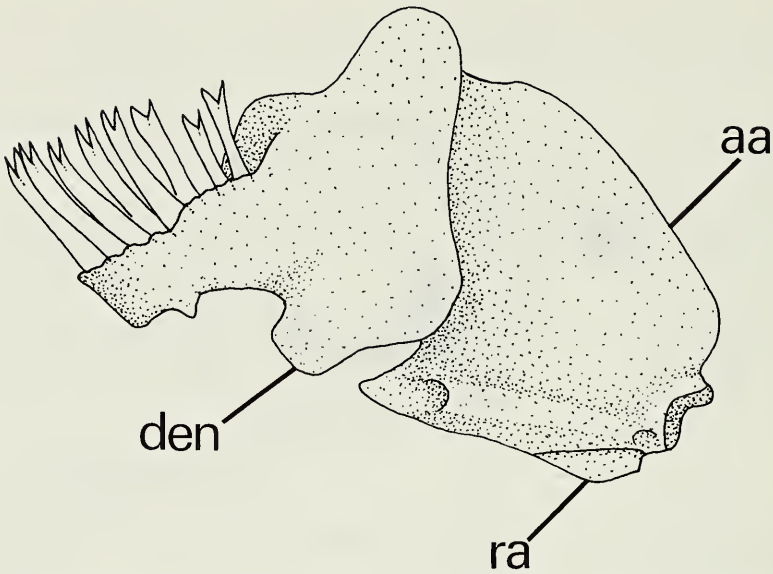

Fig. 3. Left lateral view of lower jaw of *Nannocharax maculicauda*, penultimate tooth in process of replacement; den—dentary, aa—angulo-articular, ra—retroarticular.

quarters distance to anus; pelvic-fin rays i-8-i in holotype (i-8-i in 5 paratypes, i-7-i in 2 paratypes). Caudal fin forked, with 17 branched rays, principal ray count 10/9. Adipose fin small, unscaled.

Total vertebral count including vertebrae of Weberian apparatus and fused PU_1+U_1, 41 in holotype (41 in 3 paratypes, 42 in 4 paratypes). Vertebral processes straddling dorsal aorta laterally arise from ventral surface of vertebrae 2, 3 and 4 (see Vari 1979, Fig. 30). First two full pleural ribs with proximal, posteriorly-directed flanges extending over dorsal surface of anterior gasbladder chamber. First full pleural rib with an anteriorly directed flange midway along its length; flange extends along anterolateral surface of anterior gasbladder chamber. Hypurals 1 and 2 fused into an autogenous element.

Coloration in alcohol.—Overall coloration pale yellow. Large number of dark chromatophores on dorsal and lateral portions of snout and along anterior margin of maxilla. A few scattered dark chromatophores along anterior margin of lower lip. Pale chromatophores in a dense patch over brain and visible through transparent frontals and parietals. Dorsal fin unpigmented other than for some chromatophores on last unbranched and first branched dorsal-fin rays. Caudal fin with chromatophores arranged along distal two-thirds of fin-ray margins. Anal fin with chromatophores on distal half of anterior fin rays. Pectoral and pelvic fins with a few scattered chromatophores along their distal portions. A series of chromatophores arranged longitudinally on body at base of rayed dorsal where that fin emerges from dorsal surface of body. A series of chromatophores occurs slightly lateral of midventral line, extending from between pelvic fins to rear of anal fin;

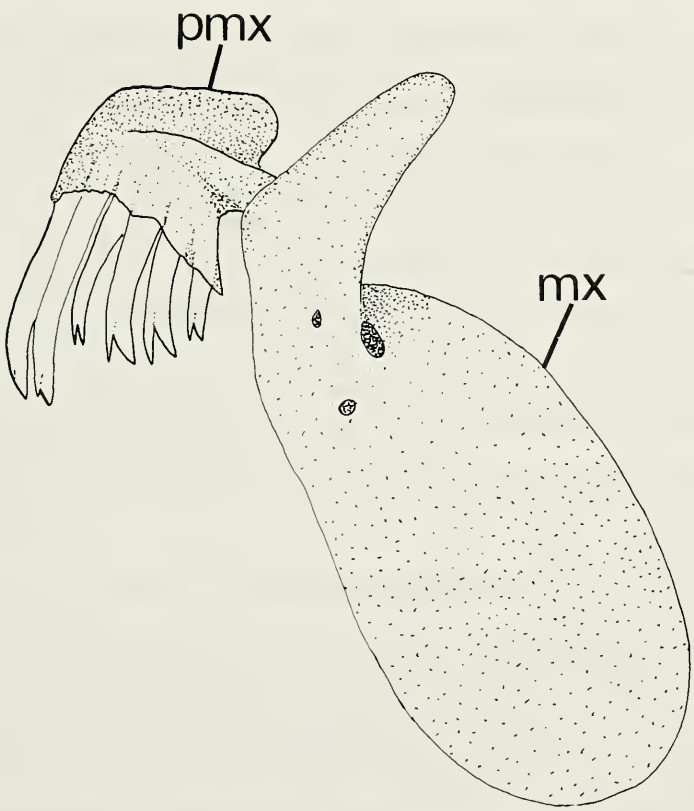

Fig. 4. Left lateral view of upper jaw of *Nannocharax maculicauda*, third premaxillary tooth in process of replacement; pmx—premaxilla, mx— maxilla.

chromatophore pigmentation most intense between anus and anal-fin origin with each lateral chromatophore series contacting its partner or being only slightly separated from it in that region. A large, strongly pigmented lateral spot on caudal peduncle and anterior portions of middle caudal rays. Spot horizontally elongate, rounded anteriorly, somewhat triangular on middle caudal rays posteriorly. Chromatophores lightly outlining scale margins on dorsal portion of body posterior to rayed dorsal fin.

Etymology.—maculicauda, from the Latin *macula,* spot, and *cauda,* tail; a noun in apposition, in reference to the caudal spot.

Relationships.—Nannocharax maculicauda possesses a series of characters derived within distichodontids (the absence of an inner row of dentary and premaxillary dentition; the absence of a laterosensory canal segment in the dentary; a horizontally expanded hyomandibula; the absence of postcleithrum 1; the fusion of postcleithra 2 and 3; anterior diverticuli of the swimbladder; a reduced, posteroventrally sloping sphenotic process; the reduction of the dorsal portion of the opercle; and a greatly reduced metapterygoid-quadrate fenestra) congruent with its placement within the monophyletic assemblage formed by *Nannocharax* and *Hemigrammocharax* within the family (Vari 1979:331). Given our poor understanding of the phy-

logenetic history of the components within the assemblage formed by *Nannocharax* and *Hemigrammocharax* it is impossible to advance a definitive hypothesis on the relationships of *Nannocharax maculicauda*. Nonetheless, it is noteworthy that this species does share derived characters (a relatively elongate body form and a partial encapsulation of the anterior chamber of the gasbladder by flanges of the first and second full pleural ribs) with at least *Nannocharax brevis, N. gobiodes, N. niloticus,* and *N. intermedius*. Further study is necessary to determine the distribution of these hypothesized derived characters within *Nannocharax* and *Hemigrammocharax*.

Remarks.—During the course of this study an additional derived character was found which distinguishes some (all?) *Nannocharax* species within the Distichodontidae. In contrast to the round pupil characteristic of most distichodontids and other characoids, the iris of *Nannocharax maculicauda* is anteriorly emarginate (Figs. 1 and 2). As a consequence the aperture of the pupil is horizontally ovoid, with this modification apparently increasing the fishes' visual field anteriorly. Within *Nannocharax* this modification also occurs in *N. seyboldi* (Schultz, 1942, pl. 35), *N. ansorgei,* and *N. altus* among species examined. A comparable correlation between an anteriorly expanded pupil and a somewhat to markedly elongate body form also occurs in the neotropical characoid genera *Ammocryptocharax* (Weitzman and Kanazawa, 1976, Fig. 1), *Klausewitzia* (Weitzman and Kanazawa, 1977, Fig. 2) and *Nannostomus* (Weitzman and Cobb, 1975, Figs. 2 and 5).

Comments on Nannocharax *and* Hemigrammocharax.—As discussed by Roberts (1967) and Vari (1979), the present distinction between *Nannocharax* and *Hemigrammocharax* is based on the completeness of the lateral line, which is of questionable value either as a diagnostic character or as an indicator of phylogenetic relationships. The present imprecision in the level of incompleteness of the lateral line that is diagnostic of *Hemigrammocharax* is reflective of this confusion. The type-species of the latter genus, *H. ocellicauda* (Boulenger), was illustrated as having only the eight anteriormost lateral line scales pored. Recently, however, Poll (1967) has included in the genus a series of species, some of which have a nearly complete series of laterosensory pores along the lateral line. Roberts (1967:252) also noted that in his material of *H. ocellicauda* the pored lateral line is not truncate as in the type, but rather "stutters." These differences in the extent of poring may be reflective of the ontogenetic variability in pored lateral line scale number reported by Jubb and Gaigher (1971:15) for *Nannocharax multifasciatus* and found in *N. maculicauda* in this study.

More significantly, a hypothesis that a "reduced" lateral line defines a monophyletic group within the assemblage formed by *Nannocharax* and *Hemigrammocharax* is incongruent with the distribution of a series of other hypothesized derived characters. Some, although not all members of each genus, (*Nannocharax niloticus, N. ansorgei, N. gobioides, N. intermedius,*

Hemigrammocharax machadoi, and *H. polli*) share the derived elimination of ossified infraorbitals 4 and 5. Similarly, an apomorphic lack of a fourth upper pharyngeal tooth plate and its associated dentition has been found in only a subunit of each genus (*Nannocharax fasciatus, N. niloticus,* and *Hemigrammocharax machadoi*). Finally, within each nominal genus there occur some species with the dorsal-fin origin posterior to the vertical through the pelvic-fin origin, another seemingly derived condition. The incongruence of the distribution of these characters with the present delimitation of *Nannocharax* and *Hemigrammocharax* together with the ontogenetic variability in the distinguishing generic character casts doubt on the monophyly of each genus. However, their redefinition along phylogenetic lines must await an in-depth analysis of the assemblage they form within the Distichodontidae.

Acknowledgments

The specimens of *Nannocharax maculicauda* which served as a basis for this study were collected during the 1964 Biological Mission to Gabon, CNRS, France. This paper represents the ninth in the series "Poissons du Basin de l'Ivindo" started by one of us (JG) in 1966. Gordon J. Howes provided information on the syntypes of *Hemigrammocharax ocellicauda*. Fig. 1 was taken by Susan Karnella. This paper benefitted by comments from Stanley H. Weitzman.

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